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HUNTERS RING DINNER BELL FOR RAVENS: EXPERIMENTAL EVIDENCE OF A UNIQUE FORAGING STRATEGY

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Abstract. We have long known that corvids are adaptively flexible in behavior, but have rarely tested their flexibility and creativity in solving problems outside the laboratory. Through a carefully controlled experiment conducted in the wild, I have found that Common Ravens (*Corvus corax*) fly toward gunshot sounds, presumably in order to locate animal gut piles left by hunters. This is the first conclusive evidence of any scavenger species pursuing gunshots. Furthermore, ravens exhibited this behavior only when gunshots were fired from within forested habitat, when the shots may be most valuable to them for locating gut piles. Interestingly, raven behaviors suggest that they may have learned the usefulness of gunshots by substituting them for other previously known sounds already used to locate food in the wild.

Key words: Cervus elaphus; *Common Raven;* Corvus corax; *elk; foraging strategy; gunshot; gut pile; hunting; rifle; scavenger; second-order conditioning.*

INTRODUCTION

Common Ravens (*Corvus corax*) follow wolves (*Canis lupus*) to eat carcass meat of wolf prey (Stahler et al. 2002, Wilmers et al. 2003) and also appear to associate with human hunters to obtain food. According to Native American and Scottish mythologies, they escorted hunting expeditions, and apparently trailed Viking ships and European military crusades to exploit remains left by the plunderers. Currently, ravens, as well as scavenging bears and eagles, migrate into game-hunting areas to feast on animal gut piles left by hunters (Davenport and Weaver 1982, Swenson et al. 1986, Haroldson et al. 2004, White, *in press*). Such behavior supports the hypothesis that human hunters replace wolves in some landscapes as the main predator providing ravens with food (Heinrich 1999). Yet, hunting techniques used by humans and wolves are conspicuously different. Most notably, humans use firearms, creating a loud bang with each kill. In their transition from wolves to humans, have ravens learned to use the gunshot sounds to their benefit?

Gunshots can signal the nearly exact location of forthcoming gut piles left by successful hunters. Yet, gunshots are typically avoided by wildlife because they represent disturbance and danger (Grubb and King 1991, Boileau 2001). Ravens, bears, and eagles were all hunted with guns throughout North America until just 30 years ago. Even though most of these scavenger species are now protected from hunting, all are long-lived, reproducing only after reaching several years of maturity. Thus, they are demographically excluded from having evolved an affinity for gunshot sounds so quickly. Instead, any significant attraction that they may exhibit toward hunter gunshots probably represents a learned foraging strategy.

METHODS

To determine if ravens cue toward hunter gunshots, I visually estimated their number within a 100 m radius of me 10 minutes before and 10 minutes after firing a 0.30-06 rifle at 12 predetermined locations within Jackson Hole, Wyoming's ungulate hunting zone (Wyoming Game and Fish [2002] hunting units 74, 75, 76, and 79) in November 2002 (i.e., during the fall hunting season). I also honked an air horn, blew a whistle, and made no sound at each testing location to isolate the gunshot sound's effect on ravens from possible effects of other sounds or from my presence. I presented the gunshot and three control treatments at each location in random order, each on a different day. No elk or hunters were near me during each trial.

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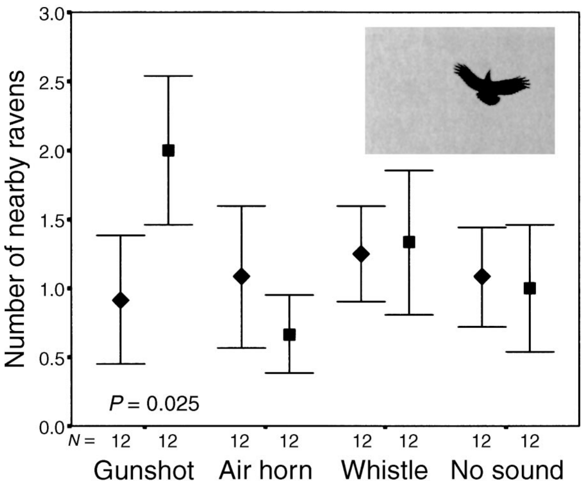

FIG. 1. Number of ravens (mean $\pm$ 1 SE detected within 100 m of the author 10 min before (diamonds) and 10 min after (squares) firing a 0.30–06 rifle (gunshot), honking an air horn, blowing a whistle, or making no sound at 12 locations in Jackson Hole, Wyoming's ungulate hunting zone during the 2002 fall hunting season. The number of nearby ravens increased significantly only after the gunshot treatment (by 1.08 ± 0.31; $t = 2.60$, df = 11, $P = 0.025$). Inset picture: raven circling author moments after a gunshot treatment.

Testing locations covered all major regions within Jackson Hole's 330-km^2 hunting area; they were 3–35 km apart from each other, with a mean nearest neighbor distance of 5.04 ± 0.63 km (mean $\pm$ 1 SE). Raven nest density in Jackson Hole is ~0.4 nests/km^2 (D. Craighead and R. N. Smith, *unpublished data*; White, *in press*), and raven abundance during the fall may be up to three times higher than that during the breeding season (White, *in press*). Thus, it is estimated that several hundred ravens were exposed to the experiment.

Differences in the mean number of ravens after vs. before each treatment were tested via a two-way repeated-measures ANOVA in which I set each testing location as a block and randomized each treatment within blocks. If heterogeneity among treatments was found, then the mean change in the number of ravens for the gunshot treatment was compared to zero via a one-sample t test, as well as to the mean change in the number of ravens for the horn, whistle, and no sound treatments through planned-contrast tests.

RESULTS

The difference in the mean number of ravens after vs. before a treatment varied among treatment types (two-way repeated-measures ANOVA, $P = 0.01$; Fig. 1), with abundance increasing significantly only after the gunshot treatment (by 1.08 ± 0.31 ravens; $t = 2.60$, df = 11, $P = 0.025$). Three planned-contrast tests with sequential Bonferroni correction found there to be a significant difference in raven response to the gunshot treatment compared to that for the horn, whistle, and no sound treatments.

Of the 12 gunshot treatments, seven resulted in a positive difference in the number of ravens within 100 m of me after vs. before the treatment. Of those seven positive responses, five contained groups of 1–4 ravens flying by within 15–100 m, and four contained groups of 1–3 ravens flying directly overhead or circling within 15 m of the gunshot location. No ravens were observed to approach and then reverse direction before being within 100 m of the gunshot location.

All seven of the positive responses to the gunshot treatment occurred at forested locations (containing >300 trees inside the 100 m radius experimental area; $N = 9$ sites), and post hoc analysis found ravens to be attracted toward gunshots fired from within forested locations only, not toward those fired in open field locations (containing <10 trees inside experimental area; $N = 3$ sites) (mean difference in number attracted = 1.89 ± 0.56 ravens; independent-samples t test, $P = 0.008$; Fig. 2).

DISCUSSION

The significant increase in the number of nearby ravens after the gunshot sound, concurrent with the absence of such a response in other contexts, clearly indicates their attraction toward the unique gunshot stimulus. Amid a sea of anecdotal observations (e.g., noted by Heinrich [1999] and by D. Tyers, [National Forest

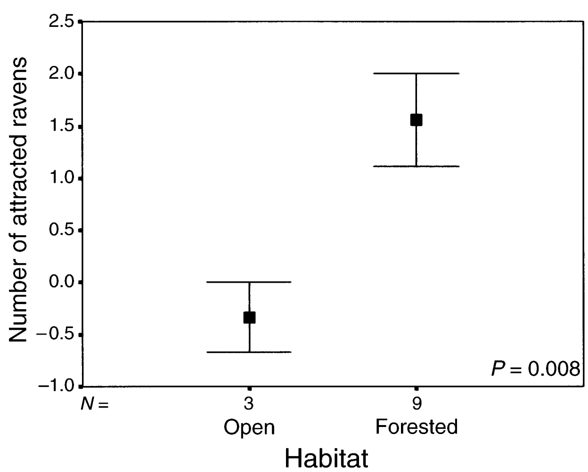

FIG. 2. Estimated number of ravens (mean $\pm$ 1 SE) attracted by the gunshot treatment (the number detected after the treatment minus the number detected before the treatment for each trial) in open (<10 trees inside 100 m radius experimental area; $N = 3$) and forested (>300 trees; $N = 9$) habitat locations. Ravens were only attracted by gunshots fired from within the forested habitat locations (independent-samples t test, $P = 0.008$).

Service] *personal communication*), this is the first conclusive evidence of any scavenger species pursuing gunshots. Recognizing that gunshots provide no known direct benefit to ravens, but that they can indicate a gut pile food source (when the hunter is successful), the results found in this experiment support the speculation that ravens cue toward gunshots in order to locate gut piles.

How did ravens learn to equate gunshots with food? Although one could argue that they constructed a new cognitive link between gunshots and gut piles (*standard classical conditioning*; Pavlov 1903), instead they may have simply associated gunshots with other sounds in the wild already known to indicate food (*second-order conditioning*; Pavlov 1927). Second-order conditioning in a foraging context has been observed across a wide variety of vertebrate taxa (Pavlov 1927, Holland and Rescorla 1975, Amiro and Bitterman 1980), including birds (pigeons; Ward-Robinson 2004). Ravens are attracted toward conspecific calls made at distant food sources (Heinrich 1988, Heinrich et al. 1993) and possibly toward wolf howling, which is often a behavioral precursor to wolves hunting (Harrington 1978). Thus, ravens already associate specific sounds with food and may have simply perceived the gunshot sound as just another dinner bell. Also, ravens are highly social, and individuals will purposely follow and lead conspecifics to hidden food sources (Marzluff and Heinrich 1991, Heinrich and Marzluff 1995, Marzluff et al. 1996) (recall that groups of up to four ravens were observed responding to the gunshot treatment). As a result, some ravens may have learned the value of the gunshot stimulus through conditioning, whereas others learned by following knowledgeable conspecifics.

Why were ravens attracted toward gunshots fired from within forested locations, but not toward those fired in the open? Several non-mutually exclusive hypotheses exist. In the open locations, ravens could probably see me (I wore bright orange and they see in color) and any elk (they are conspicuous in the open, and travel in groups) at a distance. Possibly ravens were not attracted toward the gunshots I fired in the open because they already knew my location, or that I was bluffing and had not killed an elk. Alternatively, ravens may choose to ignore all gunshots fired in the open because they can suitably survey gut pile distributions in open areas using visual cues alone. Approximately 600 elk are harvested, many in open areas, throughout the study area each fall (Wyoming Game and Fish Department 2004). Most kills result in a roughly 70-kg (Bailey 1999), conspicuously colored gut pile, and a distinct carcass drag track left by the successful hunter. Collectively, these visual cues may enable ravens to easily find gut piles in open terrain, preempting any need for them to use the acoustic gunshot cue. A third hypothesis posits that hunters may be differentially successful at ''connecting'' their shot with elk in open vs. forested landscapes. If the shot : kill success ratio is sufficiently high in the open, then the reinforcement value of the gunshot stimulus would be too low to generate a raven response (Rescorla 1988, Sangha et al. 2002). This hypothesis is related to another hypothesis (B. Heinrich, *personal communication*) speculating that ravens in northeastern USA are not attracted toward gunshots because the reinforcement value of the stimulus is diminished by both a high shot : kill ratio, and a high prevalence of bird hunters who do not leave carrion for scavengers. At the least, the observed difference in raven response to gunshots relative to the surrounding forest cover in Jackson Hole suggests that ravens are not blindly pursuing all gunshots, but are critically evaluating the context of each gunshot situation.

Considered by many to be a remarkably intelligent species capable of learning innovative foraging behaviors (e.g., Ficken 1977, Andersson 1989, Heinrich 1995, Lefebvre et al. 1997), ravens exhibited in this experiment a foraging strategy found in no other species. Beyond the basic scavenger routine of following hunters or migrating into hunting areas, ravens pursued hunter gunshots, potentially enabling them to locate gut piles with increased efficiency. Additionally, this experiment verifies the raven's close association with human hunting activities as a foraging behavior, confirms the raven's attraction toward specific acoustic stimuli representing food, and indicates its keen ability to learn novel stimuli that are analogous in meaning to other stimuli already known in the wild.

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